A FRAGMENTARY SPECIMEN OF *SAURICHTHYS* SP. FROM THE UPPER BEAUFORT SERIES OF SOUTH AFRICA

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(With 1 figure)

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ABSTRACT

The tip of an elongate jaw, found in association with the holotype of the amphibian *Capitosaurus africanus*, is identified as belonging to the actinopterygian genus *Saurichthys*. This is the first record of the family Saurichthyidae from the mainland of Africa; an additional point of interest is its almost certain freshwater provenance.

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INTRODUCTION

The specimen was discovered by Mrs Ione Rudner of the South African Museum during preparation of the holotype of the amphibian *Capitosaurus africanus* Broom, 1909 (SAM–2360). It lay in the right interpterygoid vacuity of the amphibian skull roughly at the same level as, but not in contact with, the ventral surface of the palatal bones. The protection so afforded is probably responsible for its preservation, but it is not possible to determine if there is any other significance in the association.

The specimen was subsequently freed of matrix by Mrs Rudner and tentatively identified as belonging to the genus *Saurichthys* by Dr J. Cosgriff, of Wayne State University, Detroit, U.S.A.

LOCALITY AND HORIZON

The *Capitosaurus* skull was collected by Broom from the *Cynognathus* beds of Farm Vaalbank, near Burgersdorp (Broom 1909). The Cynognathus zone comprises the whole of the Upper Beaufort Series (Broom 1932; Hotton 1967) and, according to Harland *et al.* (1967), is of Lower Triassic (Olenekian) age.

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DESCRIPTION

Order SAURICHTHYIFORMES

Family **Saurichthyidae**

Genus *Saurichthys* Agassiz, 1834

Saurichthys sp. indet.

The specimen (SAM–2360*a*) consists solely of the incomplete tip of an elongate jaw. It measures 11,8 mm in length and roughly 3,6 mm in width. In dorsal and ventral view (Fig. 1) the anterior end appears roughly rounded and behind this the two sides are more or less parallel. In lateral view the jaw is slightly curved and decreases in height anteriorly so that, whereas the tooth-bearing surface is almost flat, the opposite surface shows a more pronounced curvature that increases towards the anterior end.

The external surfaces show traces of a weak ornamentation of short, mainly longitudinal, ridges. There is no sign of a sensory canal.

The oral surface bears a narrow median ridge that projects slightly above the general level of the bone and, in places, seems to show an indistinct longitudinal suture-line. On either side of this ridge lie four large teeth or tooth-bases, arranged more or less symmetrically, and between these a number of less regularly arranged, smaller teeth. All, except one of the smallest, were damaged or missing before fossilization.

The larger teeth lie in pairs, one on each side of the midline. Their bases occupy the whole width between the median ridge and the edge of the jaw. They are conical in shape and inclined away from the sagittal plane but with a slight medial curvature so that their apices must have lain vertically above, or below, the jaw edge. The anterior pair, in addition, project slightly forwards. The remains of the best preserved large tooth measure 2,8 mm in height; when intact it must have been at least 0,5 mm taller. The apical part of the tooth is more transparent than the rest and is ornamented with fine, closely-spaced, parallel striations running in an apical-basal direction. This part is marked off from the remainder of the tooth by a barely visible groove and is estimated to have accounted for slightly more than one-third of the total height. The surface of the rest of the tooth is practically smooth except for moderate plication near the region of attachment to the underlying bone.

The small teeth are less than half the height of the large ones, about twice as numerous, and occur either singly or in groups of two or three along the edge of the jaw in the gaps between the large teeth. They appear to have been similar in shape and structure to the larger teeth but all except one are broken and abraded. The smallest tooth of all (arrowed in Fig. 1) is intact and, though no surface detail can be made out in this tooth either, examination by transmitted light with the specimen immersed in cedar-wood oil reveals some details of its internal structure. There is a distinct apical cap of clear material which is moderately birefringent and contains few tubules and is therefore identified as enameloid (Schaeffer 1977) or modified dentine (Peyer 1968). The remainder of the tooth consists of orthodentine with the characteristic, numerous, closely-spaced dentine tubules radiating from a central pulp cavity. This part shows only very slight optical activity between crossed polarizers. The pulp cavity, in its distal half at least, is relatively narrow and ends just short of the amelodentinal junction. The proximal part of the tooth is too opaque for much detail to be distinguished.

The broken end of the specimen is roughly D-shaped with a single, small,

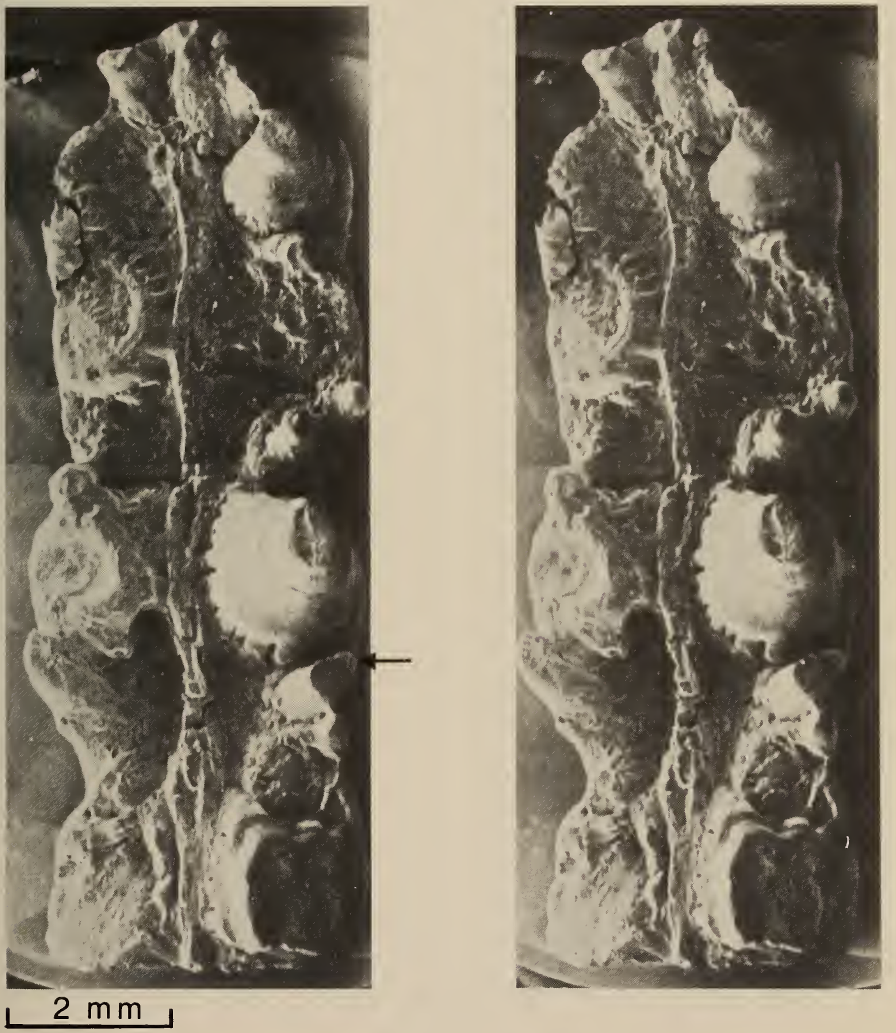

Fig. 1. Stereoscopic pair of scanning electron microscope photographs of specimen SAM–2360*a* in oral view. The arrow points to the small tooth referred to in the text.

nearly circular central cavity infilled with calcite. The bone is relatively thick but compact and shows no sign of endochondrial origin.

IDENTIFICATION

The presence of a distinct apical cap of enameloid or modified dentine clearly shows that the specimen belongs to an actinopterygian fish (Peyer 1968). With this and the conspicuous elongation of the jaw in mind there appear to be only four reasonable possibilities, that it is from: (i) a saurichthyid; (ii) an aspidorhynchid; (iii) an early representative of one of the several groups of long-jawed euteleosts; or (iv) a species unrelated to any of the known fishes with elongate jaws. These alternatives will be considered in order.

(i) In the family Saurichthyidae the two jaws are more or less equal in length. The anterior end of the upper jaw appears to be composed almost entirely of the premaxillae (rostalo-premaxillaries in Stensiö's (1925) nomenclature). These are curved transversely so as to form a tapering, hollow half-cylinder that is completed ventrally by the horizontal dental lamellae which extend medially to meet the lateral edges of the slender vomers. The resulting structure has a single cavity, as in specimen SAM–2360*a*. It seems unlikely that the vomers extended right to the tip of the jaw, and here the two premaxillae must have met ventrally as well as dorsally. Stensiö (1925) suggests that separate rostral and, or, postrostral elements were also involved but, whatever the ontogeny of this region, none of the numerous specimens belonging to several species examined by the author shows any sign of sutures dorsally though suggestions of a midventral suture are occasionally visible. The anterior end of the lower jaw appears to have been formed in a closely analogous manner from the dentaries (dentalosplenials) with a minor contribution from the coronoids (mixicoronoids) paralleling that of the vomers to the upper jaw. According to Stensiö (1925) in *Saurichthys hamiltoni* the two mandibular rami meet in a very long, rigid symphysis but do not coalesce and a distinct median ventral suture persists. However, in most species in which this region is known no sutures are visible and the tip of the mandible is so similar, apart from its inversion, to the corresponding part of the upper jaw that it is impossible to distinguish them on morphological grounds alone.

The ethmoidal and mandibular sensory canals have never been traced right to the tips of the jaws in any species and may have ended some distance short of this.

In nearly all species in which the dentition is known each half of each jaw carries a single series of fairly evenly spaced, large teeth interspersed with less regularly arranged, smaller teeth and these tooth-rows extend right to the tips of the jaws. Again there is no observable difference between upper and lower jaws. The teeth themselves do show some interspecific differences but in general are perfectly compatible in shape, proportions, ornamentation and structure with those of the specimen described above.

There are, at present, four valid genera in the family Saurichthyidae:

Saurichthys; *Saurorhynchus* Reis, 1892; *Brevisaurichthys* Beltan, 1972; and *Systolichthys* Beltan, 1972.

The genus *Saurichthys*, which contains at least thirty-five species ranging throughout the Triassic, has never been adequately defined because of the fragmentary nature of the material of the type species, *Saurichthys apicalis* Agassiz, 1834. However, several of the species ascribed to this genus are known in some detail and nothing that the author has been able to discover suggests that the specimen SAM–2360*a* does not belong to this genus.

The genus *Saurorhynchus* contains two Lower Jurassic species. Though not a diagnostic character, as it is shared with at least one species of *Saurichthys*, both species of *Saurorhynchus* show the presence of 'incissivlucken', distinct depressions in the bone of the jaw into which the apices of the large teeth of the opposite jaw fitted in occlusion. The absence of this feature in the specimen under discussion argues against it belonging to this genus.

The genera *Brevisaurichthys* and *Systolichthys* were erected by Beltan (1972) each to contain a single new species from the Middle Triassic (? Ladinian) of Spain. In both of these genera the elongation of the head is noticeably less than in *Saurichthys* and *Saurorhynchus* and the relatively obtuse ends to the jaws make it unlikely that SAM–2360*a* belongs to either.

(ii) In the family Aspidorhynchidae the upper and lower jaws are dissimilar in structure. In most species the head is continued beyond the anterior limit of the mouth as a slender, tapering rostrum which is roughly circular in cross-section and is toothless for all, or nearly all, of its length. In a few species, e.g. *Aspidorhynchus tenuirostris* Agassiz, 1833, there is no rostrum, strictly speaking, and both jaws extend to the anterior end of the head. In these species the major part of the upper jaw is formed, as in the Saurichthyidae, from the elongated premaxillae but each premaxilla is rolled into a complete, hollow cylinder and, though these meet and fuse dorsally, they remain separated ventrally for most, if not all, of their length, so forming a median groove for the reception of the presymphysial teeth. The detailed structure of the extreme tip of the upper jaw of these species is poorly known but appears to consist of a half-cylinder grooved ventrally and with its interior filled with spongy (? endochondrial) bone; a short distance behind the tip the paired, cylindrical premaxillae can clearly be recognized, so that in cross-section the upper jaw shows either two cavities or none at all. The dentition of the upper jaw differs from that of the saurichthyids and of specimen SAM–2360*a* in the segregation of the teeth into rows or groups within which all neighbouring teeth are of roughly similar size. Thus the fused premaxillae bear two principal tooth-rows composed of relatively large teeth posteriorly and these decrease in size gradually and evenly towards the tip of the jaw; smaller teeth are present on the posterior part of the premaxillae in some species but these are confined to separate rows flanking the larger teeth and never extend into the anterior part of the bone.

The anterior end of the lower jaw is formed by a single, median presymphysial bone which carries a highly distinctive dentition consisting of a single, median row of large teeth flanked posteriorly, in some species only, by one or two separate rows of much smaller teeth on either side.

The earliest known aspidorhynchid comes from the Bathonian Stage of the Middle Jurassic which does leave an appreciable time-gap, but quite apart from this it seems fairly obvious on anatomical grounds that specimen SAM–2360*a* cannot possibly belong to an aspidorhynchid.

(iii) The Euteleostei (Division III of Greenwood *et al.* 1967) include a number of fishes in which the jaws show conspicuous elongation.

In the living Belonidae (garfishes) the jaws are roughly equal in length and toothed throughout. The anterior end of the upper jaw is narrower than the corresponding part of the lower jaw and fits partly within it during occlusion. The upper jaw is formed, as in the other families described above, mainly from the elongate premaxillae, each of which is completely rolled upon itself prior to joining with its fellow so that in cross-section this jaw displays two cavities, one on each side of the midline, and, moreover, is roughly oval in shape. The lower jaw is roughly W-shaped in section with a well-developed median ridge separating two deep channels into which the teeth of the upper jaw fit. The teeth, though sharply pointed, are all relatively small and confined to the edges of the jaws. As in the Aspidorhynchidae, larger and smaller teeth are segregated and do not intermingle in the same row, and the smaller teeth do not extend to the anterior ends of the jaws. In the closely related Hemirhamphidae (half-beaks) only the mandible is elongated and this projects beyond the upper jaw as a toothless pseudorostrum. The geological record of the suborder Exocoetoidei, to which these fishes belong, is only known with certainty to extend back to the Middle Eocene though there is a doubtful record from the Cretaceous (Maestrichtian) (Patterson 1967).

The extinct suborder Alepisauroidei Rosen, 1973, contains several Upper Cretaceous genera with greatly elongated jaws. In *Ichthyotringa* Cope, 1878, *Apateopholis* Woodward, 1891, and *Dercetis* Agassiz, 1834, the two jaws are of roughly equal length; in *Rhynodercetis* Arambourg, 1944, the upper jaw is considerably longer than the lower and so forms a true rostrum. In all, the anterior part of the upper jaw is formed largely from the premaxillae with contributions from the mesethmoid, vomer and palatines, and the anterior part of the lower jaw from the dentaries (Goody 1969). The dentition in all four genera is unlike that of specimen SAM–2360*a*. In *Ichthyotringa* each half-jaw has a row of modestly-sized conical teeth and lateral to this a completely separate marginal row of minute teeth. In *Apateopholis* the premaxillary and dentary teeth are all extremely small. *Dercetis* has small, needle-like hollow teeth with peculiar apecies, and on the dentary these teeth are arranged in clusters not rows. *Rhynodercetis* has no teeth at all on the premaxillae and only small teeth on the dentary.

The Xiphiidae (swordfishes) and Istiophoridae (marlins and sailfishes) have conical rostra which project for some distance beyond the mandibles. Their lower jaws are slightly elongated but remain more or less normal in appearance and the anterior ends do not resemble SAM–2360*a*. The premaxillae are toothless for all or most of their length. Dentary teeth are either minute or absent.

The extinct family Palaeorhynchidae, grouped with the xiphiids and istiophorids in the suborder Scombroidei, contains two Lower Tertiary genera: *Palaeorhynchus* Blainville, 1818, with jaws of roughly equal length; and *Hemirhynchus* Agassiz, 1844, in which the lower jaw is shorter than the upper. In both genera the anterior parts of upper and lower jaws are circular in cross-section, solid and completely devoid of teeth.

The Upper Cretaceous and Eocene Blocidae are poorly known and, though they, too, were at one time included in the suborder Scombroidei, Patterson (1973) regards their affinities as uncertain. The upper jaw is extended into a rostrum which, according to Woodward (1901), 'resembles a pair of tubes pressed together'. The mandible is only about two-thirds of the length of the upper jaw and rostrum; very little is known of its structure. Teeth are either very minute or absent altogether.

None of the above shows sufficient resemblance to specimen SAM–2360*a* to indicate close affinity and, in any case, none can be traced backwards in time beyond the Upper Cretaceous, and it seems extremely unlikely that a representative of one of these groups, or indeed any euteleost, should have been in existence in Lower Triassic times.

(iv) The specimen may not be closely related to any of the groups discussed above. It could belong to a specialized offshoot of a group of more normal-shaped fishes, or may represent a hitherto unknown group of long-jawed fishes. As the only derived character shown by the specimen, namely the great elongation of the jaw, appears to have been independently acquired in a number of phyletic lines such speculations are impossible to prove or disprove. On the other hand, as all the observed features can be accounted for by the assumption that the specimen belongs to a species of the genus *Saurichthys* (see (i) above), these hypotheses are unnecessary and must be rejected in the interests of parsimony.

In conclusion, in all of the observed features specimen SAM–2360*a* agrees with, or falls within the range of structure shown by, the genus *Saurichthys*. There is not sufficient information to determine if it is part of an upper or of a lower jaw, to identify it as belonging to a known species of *Saurichthys*, or to warrant its description as a new species of that genus. It differs from each of the other taxa considered above in at least one character. It is unnecessary to postulate that it belongs to some previously unknown genus. The specimen is therefore determined as *Saurichthys* sp. indet.

REMARKS

There are two points which are perhaps worthy of brief comment:

(i) This is the first record of the Saurichthyidae from the mainland of Africa. According to the palaeocontinental maps produced by Smith & Briden (1977) the geographically nearest occurrences (in Triassic times) so far known are, in order: *Saurichthys madagascariensis* Piveteau, 1944, and *S. stensioi* Lehman, 1952, from the Lower Triassic (Induan) of Madagascar; *S. gigas* and *S. gracilis* (both first described by Woodward in 1890) from the Lower or Middle Triassic, and *S. parvidens* Wade, 1935, from the Middle Triassic of New South Wales, Australia; numerous Lower, Middle and Upper Triassic and Lower Jurassic species from Europe. The saurichthyids appear to have had an almost world-wide distribution and their previous absence from records for South Africa probably merely reflects the paucity of fossiliferous marine deposits of suitable age.

(ii) The Upper Beaufort Series are generally accepted as being continental freshwater fluviatile and lacustrine deposits and, though Hotton (1967) suggests that these conditions alternated with persistent deltaic ones, Rayner (1971) regards this hypothesis as untenable. The saurichthyids appear to have been predominantly marine though a few species have been recorded from deposits thought to have been laid down under fresh or 'brackish' water conditions. Specimen SAM–2360*a* could have been reworked from earlier, marine beds such as the marine phases of the Ecca or Dywka Series, but as no saurichthyid has ever been recorded there this seems improbable. It therefore appears that some species of saurichthyid were at least capable of temporary excursions into fresh water and may even have lived there permanently.

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